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Melittophily in *Drumstick tree, Moringa oleifera* (Moringaceae) and myrmecophily in Curry Leaf tree, *Murraya koenigii* (Rutaceae)

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ABSTRACT

Moringa oleifera is a deciduous tree species while *Murraya koenigii* is a semi-deciduous tree species. In both, the flowers are hermaphroditic and nectariferous offering both pollen and nectar as floral rewards. Carpenter bees are the principal pollinators in case of *M. oleifera* and ants are the exclusive pollinators in case of *M. koenigii*. Honey bees act as additional pollinators of *M. oleifera* only. In certain urban areas, sunbirds also act as most efficient pollinators of *M. oleifera*. A three-striped palm squirrel is the consistent feeder of *M. oleifera* and its feeding activity has a negative effect on the reproductive success of the tree. In *M. koenigii*, delayed spontaneous autogamy is functional due to the operation of herkogamy for sometime during the flower life facilitating the maximization of geitonogamy with ants as pollinating agents. The cultivation or planting of *M. oleifera* and *M. koenigii* in urban areas of India is a common practice. The study recommends the promotion of cultivation of both species as a part of green belt development to meet vegetable requirement in the form of their leaves and pods in case of *M. oleifera* and in the form of leaves in case of *M. koenigii*. The positive side effect of their cultivation in urban ecosystems is that they play a prominent role in the sequestration of carbon dioxide and other pollutants in the process of natural cleaning up of the polluted air.

Keywords: *Moringa oleifera, Murraya koenigii*, hermaphroditism, protandry, melittophily, myrmecophily, spontaneous autogamy.

1. INTRODUCTION

The genus *Moringa* has 13 species which include *M. arborea, M. borziana, M. concanesis, M. drouhardii, M. hildebrandtii, M. longituba, M. ovalifolia, M. peregrine, M. pygmaea, M. rivae, M. ruspoliana, M. stenopetala* and *M. oleifera* (Mahmood et al. 2010). The name "*Moringa*" is derived from "murungai, the Tamil word for drumstick (Singh 2015). *M. stenopetala* commonly called

"cabbage tree" is deciduous and endemic to northern Kenya and Ethiopia in East Africa. Many characteristics are common in *M. stenopetala* and *M. oleifera*. Both species have similar medicinal uses and have high content of oil in their seeds (Grubben and Denton 2004). In Ethiopia, *M. stenopetala* has different ecotypes and varieties, cultivated as an indigenous vegetable crop in regions where soil chemistry is favorable (Abuye et al. 2003; Demeulenaere 2001; Jahn 1991; Maundu et al. 1999). *M. oleifera* commonly called "drumstick tree" is native to Sub-Himalayan tracts of North India (Jahn 1991). It is a perennial deciduous tree which is valued for its leaves, pods and seeds for centuries. The leaves and pods are edible, have food and economic value and has often been noted as a nutritional and medicinal cornucopia. It is widely cultivated in several countries including Ethiopia, Sudan, India and the Philippines. Lately, it is being cultivated in almost all tropical countries where this tree is ideal for its growth. Different authors reported on the mating system and pollinators of *M. oleifera*. This tree species is facultative xenogamous with cross-pollination mode being the dominant (Jyothi et al. 1990). It is pollinated by honey bees and carpenter bees in central Israel (Vaknin et al. 2021), sunbirds in Asia but honey bees and carpenter bees as potential pollinators in West Africa (Krieg et al. 2017), carpenter bees and digger bees in Andhra Pradesh (Jyothi et al. 1990), carpenter bees as most efficient pollinators in Tamil Nadu (Sowmiya et al. 2018), *Apis* bees as superior pollinators in Tamil Nadu (Haran and Srinivasan 2021), and *Apis florea* as an important pollinator in arid regions of Rajasthan (Bhatnagar et al. 2018). These reports indicate that different bee groups and also sunbirds are involved in the pollination of *M. oleifera*. Keeping this information in view, the present study was executed to record the all-time actual pollinators according to the floral traits of *M. oleifera*.

The genus *Murraya* named after a Swedish physician and botanist Johann Andreas Murray is assigned with 14 globally identified species. Of these, only 2 species, *M. koenigii* and *M. paniculata* are distributed in India. The species name of *M. koenigii* is named after the botanist Johann Konig (Ajay et al. 2011; Dineshkumar et al. 2012). *M. koenigii* is naturally distributed in the east and south part of India, Pakistan, Sri Lanka and China but it is widely cultivated in Southeast Asia and also in some tropical parts of Australia and United States of America (Khosa and Prasad 1972). It is valued for its characteristic aroma and bioactive compounds and known for its role in the promotion of appetite and digestion. The leaves are used as an essential ingredient in curries for adding flavour due to their aromatic nature (Dhore 2020). The principal chemical compounds contributing to flavor and aroma are sabinene, pinene, caryophyllene, cardinol and cardinene (Bhusal and Thakur 2021). But, the whole plant is valued for use as tonic, stomachic and in various traditional uses (Ajay et al. 2011; Bhusal and Thakur 2021). The essential oils extracted from the plant are useful in the production of sun protection creams and erythema formulations, and for aromatherapy in cosmetic and soap industries (Jain et al. 2017). The extract obtained from the stem part is used in making creams to improve rough skin and skin glow (Dhongade et al. 2013). Despite the medicinal and commercial importance of *M. koenigii*, its pollination biology and scope for cultivation in farmlands and urban lands have not been examined. However, there are a couple of studies that documented the foragers/pollinators of *M. koenigii.* Bhatnagar et al. (2018) reported that *M. koenigii* is visited by bees *Apis dorsata, A. florea* and *Xylocopa fenestrata*, wasps *Vespa orientalis, Polistes hebraeus*, and butterflies *Papilio demoleus, P. polytes* and *Pachliopta aristolochiae*. Of these, *Apis* bees are pollen and nectar gatherers while all others are nectar gatherers only. But, these authors have not described their role in effecting pollination. Dhore (2020) reported that *M. koenigii* is visited by *Apis* bees, *A. florea, A. cerana indica, A. mellifera, A. dorsata*, and by butterflies *Borbo cinnara, Catopsilia pyranthe, Pachliopta aristolochiae* and *Hypolimnas bolina* but only bees have been noted as the frequent visitors and effective pollinators. The information documented in the reports of these authors does not provide any further details of sexual reproduction. Therefore, the present study is an occasion to provide certain details of floral aspects, sexual system and pollination of this tree species, and also to provide a brief note on the scope for the promotion of *M. koenigii* for cultivation in farmlands and urban lands.

2. MATERIALS AND METHODS

Moringa oleifera and *Murraya koenigii* cultivated in Arilova and Mudasarlova areas in Visakhapatnam city, Andhra Pradesh, India, were used for study during July 2021 to June 2022. Floral morphological traits were recorded for both species. The anthesis time, anther dehiscence time, sexual system, mating system and pollinators were carefully observed. Nectar characters were examined according to the methods described in Dafni et al. (2005) book. Pollinators included insects and sunbirds; their flower visiting activity, flower probing for floral rewards and role of individual species in effecting self- or cross-pollination were observed at live plants to record the pollinators. Squirrel activity was observed on the flowers of M. oleifera. The role of the observed squirrel in the sexual reproduction of this tree was also recorded. Fruit and seed features were recorded briefly.

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3. RESULTS AND DISCUSSION

***Moringa oleifera* Lamk**

It is a deciduous tree species which displays leaf fall and fushing, flowering and fruiting events at least thrice a year according to soil nutrient status and local weather conditions. It produces tripinnate compound feathery leaves. The flowers are borne in axillary paniculate cymes which produce several clusters of flowers. The floral buds in these cymes are open within two weeks; they are open daily during 0500-0900 h and the anthers dehisce longitudinally shortly before anthesis (Figure 1a). The flowers are white, pleasantly fragrant, zygomorphic, nectariferous, hermaphroditic and protandrous. The calyx consists of five small green sepals. The corolla consists of two small and three long free petals forming a cup-like structure basally to contain nectar. The androecium consists of five fertile stamens with hairy filaments and yellow anthers producing cream-colored pollen. The style is simple and placed almost at the height of anthers. Individual flowers produce 3.82-4.35 µl with 34-38% sugar concentration; nectar volume is little more and sugar concentration is little less during wet and winter seasons. The nectar volume is less and sugar concentration is more during dry season. The fruit is a trilobed-capsule or pod with several seeds. Growing pods are green and turn brown when mature and dry. The seeds are round and possess semi-permeable brownish seed hull.

Figure 1. *Moringa oleifera:* a. Inflorescence with buds and flowers, b. *Apis dorsata* collecting nectar, c. *Apis cerana* collecting nectar, d. *Xylocopa latipes* collecting nectar, e. *Xylocopa pubescens* collecting nectar, f. & g. *Funambulus palmarum* feeding on flowers.

The flowers were foraged in a legitimate way exclusively by honey bees (*Apis dorsata* –Figure 1b, *A. cerana*- Figure 1c and *A. florea*) for pollen and nectar collection and carpenter bees (*Xylocopa latipes* –Figure 1d and *X. pubescens*-Figure 1e) for nectar collection. The floral nectar and pollen are exposed to sunlight and this situation facilitates the honey bees to gather both floral rewards with great ease. The carpenter bees gathered only nectar despite having easy accessibility to pollen. Both categories of bees visited the flowers day-long with more foraging activity during forenoon time due to the availability of fresh floral rewards in addition to the leftover floral rewards from the flowers that opened on previous day(s). The upright mode of flower probing by bees and the placement of sex organs almost at the end of petals facilitate the occurrence of pollination as there is a contact between the bee body and sex organs during probing for floral reward collection. As honey bees require huge volume of both pollen and nectar and carpenter bees need more nectar for their body maintenance, especially in male sex, they visit numerous flowers on the same and different trees to meet their food requirement and in this process, they effect both self- and cross-pollination.

In *M. oleifera*, the attraction unit appears to be the entire flower and the attraction is increased by the aggregated form of flower production in paniculate cymes. Further, the flowering patches on individual trees are very prominent and act as effective advertising units at long distances to attract foragers. Once drawn towards the flowering field, the visitors, step by step, attend to the flowering branches, individual inflorescences and eventually individual flowers for collecting floral reward(s) (Dafni et al. 1997). The paniculate cymes with clusters of flowers contribute to reduction in flower search time and energy expenditure for the visiting honey bees and carpenter bees to *M. oleifera* flowers. Such a situation is economical for the bees to collect the forage efficiently with great speed and for the plant to promote self- and cross-pollination rate by the visiting bees. Earlier workers reported the function of entomophily involving different insect groups in *M. oleifera*. Jyothi et al. (1990) reported that *M. oleifera*

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flowers attract carpenter bees, digger bees, honey bees, butterflies and hawkmoths which collect either pollen or nectar or both according to their requirement. Of these, only carpenter bees and digger bees are pollinators while all others are mere foragers and have no role in pollination. Krieg et al. (2017) reported that *M. oleifera* is pollinated by sunbirds in Asia but by honey bees and carpenter bees are potential pollinators in West Africa. These authors also stated that stingless bees also visit the flowers of *M. oleifera* but it is not known whether they are nectar robbers or pollinators. Sowmiya et al. (2018) recorded 27 species of pollinator insects which included bees, wasps, flies, butterflies and diurnal hawkmoths on *M. oleifera*. Of these, carpenter bees of the genus *Xylocopa* are reported to be the most efficient pollinators in Tamil Nadu. Bhatnagar et al. (2018) reported that *M. oleifera* is visited by honey bees, carpenter bees, digger bees, leafcutter bees, wasps and butterflies. Of these, the honey bee, *Apis florea* is reported to be an important pollinator despite being small in size in the arid region of Rajasthan. Haran and Srinivasan (2021) reported that the cultivated *M. oleifera* in Tamilnadu is pollinated by bees, wasps, flies and butterflies of which *Apis* bees are treated to be the superior pollinators group just because of their abundance on the flowers. Vaknin et al. (2021) reported that honey bees and carpenter bees are involved in the successful pollination of *M. oleifera* plantations in central Israel. The present study indicates that *M. oleifera* is in principle melittophilous with carpenter bees as most appropriate and efficient pollinators. Among honey bees, *A. dorsata* is the most efficient pollinator while the occurrence of pollination by other two bees is related to their orientation in relation to the floral sex organs. Because, the medium-sized *A. cerana* and small-bodied *A. florea* do not establish contact with the floral sex organs in every visit. The second author also observed the sunbirds, *Nectarinia asiatica* and *N. zeylonica* visiting the flowers of *M. oleifera* in certain urban areas where this tree species is cultivated in residential locations for their leaves and pods. These sunbirds are very efficient pollinators of this tree species because they are quite appropriate in establishing contact with the floral sex organs while probing the flowers for nectar. Therefore, *M. oleifera* is principally carpenter-bee pollinated while all other bees and insects collectively act as additional pollinator group. The sunbirds when use this tree species as nectar source during its flowering season act as efficient pollinators while withdrawing nectar from the flowers.

In this study, a three-striped palm squirrel, *Funambulus palmarum* is a consistent voracious flower-feeder during each spell of flowering period (Figure 1f,g). It removes flowers and eat the petals and nectar-holding floral part; its flower-feeding activity is very prominent during forenoon period due to the addition of fresh flowers with fresh nectar. This flower-feeding activity has a negative effect on the success of sexual reproduction through which pod set occurs.

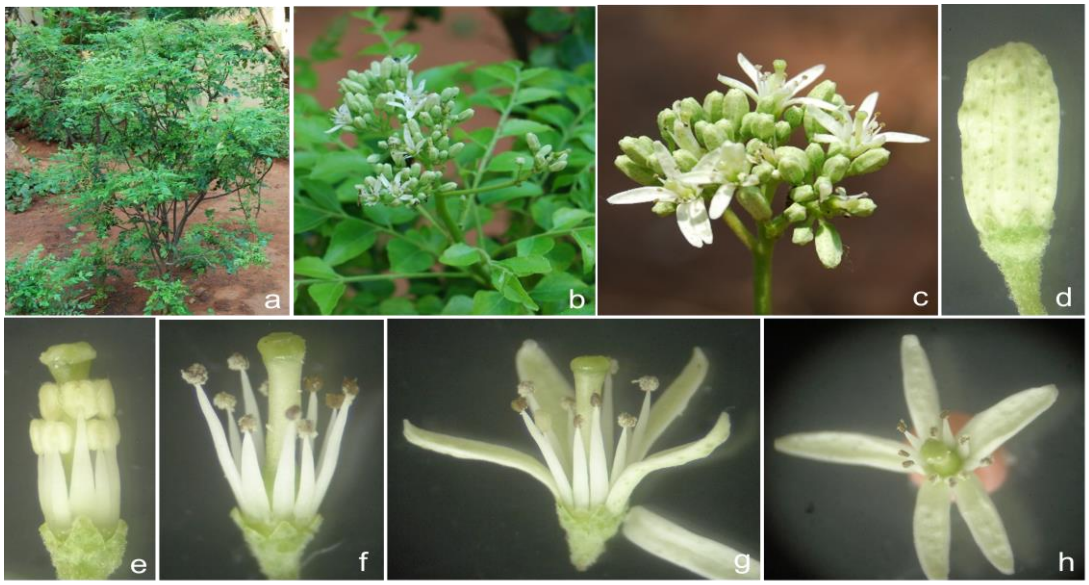

Figure 2. *Murraya koenigii*: a. Tree with fully developed leaves and partial flowering, b. Flowering inflorescences, c. A single inflorescence in flowering mode, d-h. Different stages of bud and flower.

***Murraya koenigii* (L.) Spreng.**

M. koenigii is a semi-deciduous aromatic tree species with a strong woody stem. It is leafless during winter period while it shows leaf flushing during dry season with vigorous growth, flowering and fruiting during wet season (Figure 2a,b). The leaves are odd-pinnately compound with 10-13 short-stalked ovate to lanceolate glandular aromatic leathery leaflets arranged alternately. The

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inflorescence is a terminal or axillary panicle with 58 to 87 flowers (Figure 2c). The flowers are pedicellate, small, white, fragrant, funnel-shaped and bisexual (Figure 2d-h). The calyx is hairy, green, tubular at base and apically 5-lobed sepals. The corolla is white and consists of 5 free linear-oblong petals dotted with glabrous glands. The stamens are 10 with filaments dilated at their base and tipped with dorsifixed anthers which dehisce longitudinally to release tricolporate pollen grains (Figure 3a,b); they are arranged in two whorls, each with five stamens. Further, the stamens vary in their size with two sizes of anthers in each whorl; the long and semi-long anthers have the possibility to contact the capitate stigma while the mid- and short-sized anthers have no possibility to contact the stigma. The ovary is 2-celled with a single ovule (Figure 3e). The style is green and linear with a capitate sticky stigma (Figure 3c,d). The fruit is a small black shining 1-seeded fleshy berry displaying orange, red or black color at different stages of its development and maturation.

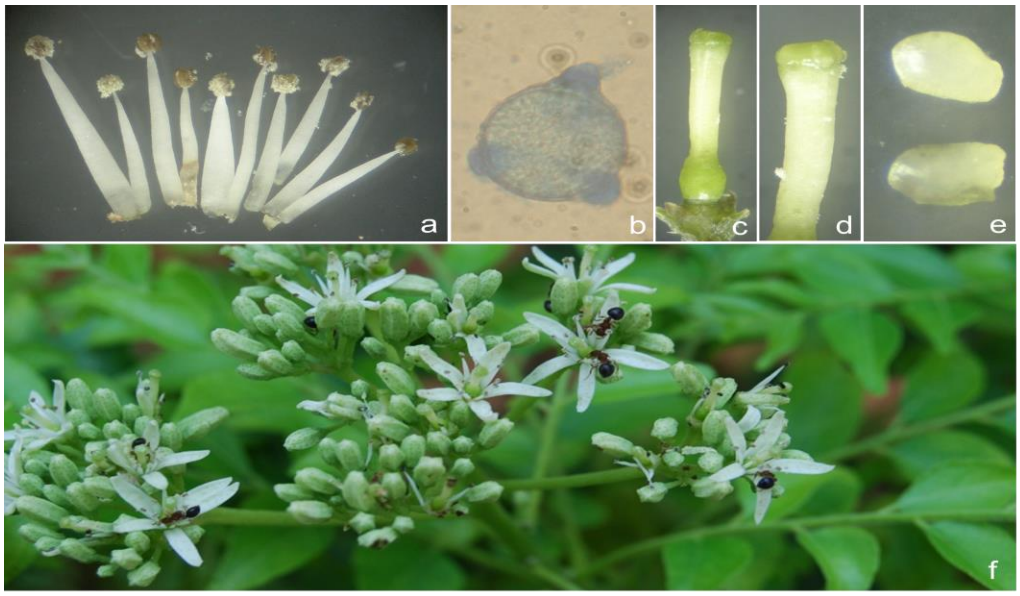

Figure 3. *Murraya koenigii*: a. Stamens with dehisced anthers, b. Pollen grain, c. Pistil, d. Style and stigma, e. Ovules, f. *Crematogaster* sp. collecting nectar.

Jain et al. (2017) reported that *M. koenigii* grows throughout the year in tropical regions. The present study found that leaf fall, leaf flushing, flowering and fruiting are sequential in occurrence but there are also anomalies in the occurrence of these events. Certain trees display flowering in dry season while most of the trees display leaf flushing and sexual events during wet season. Such a variation could be attributable to the soil conditions, age of the tree and weather conditions that exist in the habitat. The flowers being white, nectariferous and aromatic with sex organs completely exposed facilitate any forager to access both nectar and pollen. It is observed that the mature buds open early in the morning and remain so for 2 or 3 days depending on ambient weather conditions. The bisexual condition of the flowers is quite advantageous for the foragers that seek pollen and nectar from the same flower. Bhatnagar et al. (2018) reported that bees, wasps and butterflies use *M. koenigii* flowers as food source; the first category uses both pollen and nectar while the other categories use only nectar. These authors did not mention whether they effect pollination or not, if so whether all these foragers as pollinators or not. Dhore (2020) reported that bees and butterflies use *M. koenigii* as food source but only bees are frequent visitors and effective pollinators. In this study, only *Crematogaster* ants (Figure 3f) visited the flowers of *M. koenigii* despite the presence of different wild bees and butterflies in the study area. These ants were resident foragers and visited the flowers by crawling all over the tree for nectar collection. Since flowers are of open type with exposed sex organs, the ants probed the flowers without any difficulty and accessed the nectar location with great ease. In this probing, the ventral side of the ant body had contact with the stamens and the well developed capitate stigma; such a contact facilitated the occurrence of either vector-mediated autogamy or geitonogamy. The floral architecture, the function of herkogamy and the stamens of different heights collectively provide opportunities for vector-mediated self- and/or cross-pollination. Further, the close proximity between long and semi-long anthers and the capitate stigma facilitate the occurrence of spontaneous autogamy while the placement of all other anthers well below the height of the stigma simply precludes this mode of autogamy. The differential height of stamens in the flowers appears to be self-developed mechanism to minimize spontaneous autogamy and provide maximum opportunities for

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vector-mediated pollination. The fruiting observed on isolated trees in the study area in the absence of flying flower visitors is a clear case of the function of mixed mating system in the hermaphroditic flowers of *M. koenigii*. Further, the function of spontaneous autogamy is advantageous for isolated trees of this species to set fruit and seed. Jain et al. (2017) reported that *M. koenigii* is self-pollinated. The present study substantiates the same. Therefore, *M. koenigii* with hermaphroditic sexual system is self-compatible, self-pollinating, facultative xenogamous and myrmecophilous also.

India is a regular exporter of fresh and dried leaves of *M. koenigii* to Gulf and European countries and in the process, it is earning foreign exchange to a considerable level. Local markets sell the fresh leaves of this tree almost throughout the year. In view of its regular use as curry leaf, it encouraged many marginal and small farmers to raise this tree as a monocultural crop. Since the leaves of this tree species have high medicinal, culinary and export value, it is a promising candidate for local farmers to cultivate it as a commercial or cash crop and also for people living urban areas to plant or cultivate it for domestic use in personal land spaces and public lands which are vacant and noted used for any other purpose. Its cultivation in urban and also in sub-urban areas could contribute to sequestration of carbon dioxide and other pollutants and at the same time provides fresh curry leaf for culinary uses.

4. CONCLUSION

Moringa oleifera is a deciduous tree species which displays leaf fall and fushing, flowering and fruiting events at least thrice a year according to soil nutrient status and local weather conditions. The flowers are nectariferous, hermaphroditic, protandrous and pollinated principally by carpenter bees and additionally by honey bees. Sunbirds also act as efficient pollinators in certain urban areas where this tree species is cultivated for their leaves and pods. A three-striped palm squirrel *Funambulus palmarum* consistently removes flowers and eats the petals and nectar-holding floral part; its flower-feeding activity has a negative effect on the success of sexual reproduction through which pod set occurs. *M. koenigii* is a semi-deciduous aromatic hermaphroditic, facultative xenogamous tree species. The flowers at the study area attract only *Crematogaster* ants and these ants as residents on the plant act as exclusive pollinators which could effect only autogamy and geitonogamy due to their crawling nature. The flowers are herkogamous and delay spontaneous autogamy to maximize geitonogamy.

The cultivation or planting of *M. oleifera* and *M. koenigii* in urban areas of India is a common practice. The study recommends the promotion of cultivation of both species as a part of green belt development to meet vegetable requirement in the form of their leaves and pods in case of *M. oleifera* and in the form of leaves in case of *M. koenigii*. The positive side effect of their cultivation in urban ecosystems is that they play a prominent role in the sequestration of carbon dioxide and other pollutants in the process of natural cleaning up of the polluted air.

Authors contributions:

All three authors contributed equally.

Ethical approval

Melittophily in *Moringa oleifera* (Moringaceae) and myrmecophily in *Murraya koenigii* (Rutaceae) was observed in the study. The ethical guidelines for plants & plant materials are followed in the study for sample collection & identification.

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Conflicts of interests

The authors declare that there are no conflicts of interests.

Data and materials availability

All data associated with this study are present in the paper.

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